

CHROMOSOME NUMBERS OF CALIFORNIAN DELPHINIUMS AND THEIR GEOGRAPHICAL OCCURRENCE¹

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The genus *Delphinium* is represented in California by about twenty-six species. Several of horticultural interest have been studied by Mehlquist; others have been studied extensively with respect to their interfertility and evolutionary relationships by Lewis and Epling. In the course of these investigations most of the California species of *Delphinium* have been examined cytologically and a summary of our combined observations on chromosome numbers (Table I) and cytological behavior is presented here.

The materials used were either squash preparations of buds fixed in 1:3 acetic alcohol and stained in aceto-orcein or sectioned root tips fixed in CRAF and stained in safranin-gentian violet. These buds and roots were collected in the field or were taken from wild transplants grown in the garden.

CYTOLOGICAL OBSERVATIONS

The basic haploid chromosome number in the genus *Delphinium* is 8 (Darlington & Janaki-Ammal, 1945). We have found no deviations from this basic number although three of the species examined, *D. variegatum*, *D. hansenii*, and *D. gypsophilum*, have tetraploid races (Table I). The karyotypes of *Delphinium* species are morphologically very similar (Langlet, 1927; Tjebbes, 1927; Lewitsky, 1931; Lawrence, 1936; Gregory, 1941). Each genome has two long chromosomes, four of intermediate length and two quite short ones. The centromeres of the long chromosomes are submedian; those of the remainder, subterminal. The relative lengths at mitotic metaphase of each chromosome and the positions of their centromeres are shown diagrammatically in fig. 1A. This diagram is based upon measurements from root tips of *D. hansenii*, *D. parishii*, *D. hesperium*, *D. variegatum*, *D. parryi*, *D. gypsophilum*, and *D. recurvatum*. Chromosomes *a* and *b* are readily distinguishable during mitosis or meiosis by the relative lengths of their two arms. Chromosomes *c*, *d*, and *f* are difficult to distinguish from each other in mitotic divisions and are indistinguishable in meiosis. Chromosome *e* can usually be recognized in somatic divisions by the presence of a small satellite at the end nearest the centromere but usually can not be told from *c*, *d*, and *f* during meiosis. The two short chromosomes can usually be recognized by their small size but cannot always be distinguished from each other.

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¹This paper represents a report of two largely separate studies, one by Mehlquist and Wyckoff in order to provide in one place more complete data than would otherwise have been possible. Mehlquist while at the University of California, and one by Lewis and Epling. The combination was made in 1945 and Wyckoff is largely responsible for the mitotic counts on the accessions credited to Mehlquist alone or Mehlquist and others. Lewis and Epling are responsible for the remainder of the cytological data and all systematic determinations.

The tetraploid races of *D. variegatum*, *D. hansenii* and *D. gypsophilum* have indistinguishable karyotypes and differ from the diploids only in the double number.

Meiosis has been studied in pollen mother cells of 45 diploid transplants and 36 tetraploids as follows:

Diploids	Tetraploids
<i>D. gypsophilum</i> (1)	<i>D. gypsophilum</i> (4)
<i>D. hansenii</i> (20)	<i>D. hansenii</i> (22)
<i>D. hesperium</i> (4)	<i>D. variegatum</i> (10)
<i>D. inopinum</i> (3)	
<i>D. parishii</i> (1)	
<i>D. parryi</i> (6)	
<i>D. recurvatum</i> (3)	
<i>D. umbraculorum</i> (3)	
<i>D. variegatum</i> (4)	

TABLE I

	2n chromosome number	Number of populations	Number of plants
<i>D. andersoni</i> Gray	16	3	8
<i>D. californicum</i> T. & G.	16	2	10
* <i>D. cardinale</i> Hook.	16	6	26
<i>D. decorum</i> Fisch. & Mey. ssp. <i>Tracyi</i> Ewan	16	2	8
<i>D. glaucum</i> Wats.	16	1	6
<i>D. gracilellum</i> Greene	16	1	1
<i>D. gypsophilum</i> Ewan	{ 16 { 32	{ 16 { 19	{ 156 { 222
<i>D. hansenii</i> Greene	{ 16 { 32	{ 66 { 16	{ 437 { 143
<i>D. hesperium</i> Gray	16	11	30
<i>D. hesperium</i> f. <i>pallescens</i> Ewan	16	14	71
<i>D. hesperium</i> var. <i>cuyamacae</i> (Abrams) Jeps.	16	1	9
<i>D. inopinum</i>	16	3	6
† <i>D. nudicaule</i> T. & G.	16	7	26
<i>D. nuttallianum</i> Pritz.	16	1	5
<i>D. parishii</i> Gray	16	25	65
<i>D. parryi</i> Gray	16	32	104
<i>D. parryi</i> ssp. <i>seditiosum</i> (Jeps.) Ewan	16	11	21
<i>D. parryi</i> var. <i>blochmanae</i> (Greene) Jeps.	16	4	24
<i>D. patens</i> Benth.	16	11	29
<i>D. polycladon</i> Eastw.	16	1	1
<i>D. purpusii</i> Brandg.	16	3	9
<i>D. recurvatum</i> Greene	16	3	17
<i>D. trolliifolium</i> Gray	16	5	10
<i>D. uliginosum</i> Curran	16	1	10
<i>D. umbraculorum</i>	16	8	22
<i>D. variegatum</i> T. & G.	{ 16 { 32	{ 22 { 6	{ 99 { 28
		Tot. 301	Tot. 1603

*Previously reported by Mehlquist et al. (1943).

†Previously reported by Gregory (1941).



Fig. 1. A, diagram of the relative lengths of mitotic metaphase chromosomes representative of a species complex referred to in the text. B, representative meiotic metaphase I of a diploid (*D. parishii*). C, anaphase I of a diploid showing a bridge and fragment (f). The bridge involves chromosomes *a* or *b* (*D. parryi*). D, anaphase I of a tetraploid showing delayed separation of chromosomes *a* or *b* (*D. gypsophilum*). E, representative metaphase I of a tetraploid showing 12 bivalents, 1 quadrivalent ring, and 1 quadrivalent chain (*D. variegatum*).

Chiasma frequencies observed at diplotene are nearly constant for all the species examined and agree with those previously reported for *D. cardinale* (Mehlquist et al., 1943). The longest chromosome, *a*, has a chiasma frequency close to 1.0 for each arm. However, a chiasma in only one arm is sometimes found and a second chiasma may occasionally occur in one or both arms. More than two chiasmata per arm have not been observed. Chromosome *b* has a chiasma frequency close to 1.0 in the longer arm; one is usually present in the shorter arm but its precise frequency has not been determined. Chromosomes *c*, *d*, *e*, *f*, *g* and *b* generally have but one chiasma per bivalent, which is in the long arm, although an additional chiasma may rarely occur in the short arm.

Eight bivalents occur regularly in the diploids at metaphase I, but quadrivalents are frequent in the tetraploids. In 418 tetraploid cells, 183 (44 per cent) had 1 quadrivalent, 144 (34 per cent) had two quadrivalents, and no cells had more than two. The quadrivalents were confined to the two long chromosomes *a* and *b*, the former being quadrivalent in 70 per cent of the cells examined and the latter in 44.5 per cent. Of the possible quadrivalent types (Darlington, 1937) only a simple ring of four or a chain of four has been found (fig. 1E).

Disjunction of the quadrivalents at anaphase may result in either adjacent or alternate chromosome separation (fig. 1E). However, configurations indicating alternate separation are about twice as numerous as those indicating adjacent separation. Either type of separation produces nearly 100 per cent visibly good pollen and the plants concerned are fully fertile. Trivalents have rarely been observed between any of the chromosomes.

The shortest chromosomes frequently separate precociously and can often be seen as univalents at diakinesis, indicating either that no chiasmata were formed or that terminalization and separation occurred during prophase. Segregation of these chromosomes is usually equal, although it is occasionally 3 and 1 in the tetraploids. Diploid gametes carrying an extra short chromosome can function, for at least one plant grown in the greenhouse had an extra *b* chromosome. Unequal segregation of this pair in diploids apparently results in non-functional gametes.

Terminalization of chiasmata is usually complete in the six shorter pairs at metaphase I but is often incomplete in one or both arms of chromosomes *a* and *b* (fig. 1B). Sometimes separation of these chromosomes is greatly delayed at anaphase I in both diploids and tetraploids (fig. 1D). In this case the unseparated ends of the chromosomes remain on the equator until after the centromeres have reached their respective poles. The chromosomes are stretched thin and are obviously under tension, but there is no evidence in subsequent stages that breakage or abnormal separation occurs. It has been shown on a number of occasions that terminalization of chiasmata is arrested by changes in homology (Sansome, 1932; Catcheside, 1932; Darlington, 1937) and, further, that such an arrest need not lead to breakage of chromatids (Darlington, 1931). Stretched chromosomes showing delayed separation have recently been found by Marta Walters (1950) in the hybrid *Bromus trinii* \times *B. maritimus* where she has suggested that the delayed

separations may be due to changes in homology of the chromosomes. In the present instance the anaphase stretching may result from the formation of chiasmata in inversion heterozygotes, but proximal to the inversions. This is further suggested by the fact that the delayed separations are often observed in the same plants that show inversion bridges.

Pachytene has been difficult to study in our preparations. Our observations on the occurrence of inversions is accordingly based upon the anaphase. Bearing this in mind, it would seem that most of the inversion bridges apparently involve the longer chromosomes, but it has not been possible to determine either the number of inversions or the particular chromosomes in which they occur.

Anaphase bridges characteristic of those produced by crossing over within an inversion were found in 10 (22 per cent) of the diploids examined and 25 (70 per cent) of the tetraploids. In many instances the accompanying fragment was clearly visible (fig. 1C); in others it may have been obscured by other chromosomes. It is probable that inversions were present in more plants than is indicated inasmuch as bridges in plants where they did occur were seen in only 0.8–1.7 per cent of the anaphase and telophase cells examined. The possibility of inversions passing unnoticed if a limited number of cells can be examined is, therefore, very great.

In view of the high frequency of inversion heterozygotes found in them the tetraploids may carry still other inversions than those of their corresponding diploids. However, even if the diploids and tetraploids do not differ in the particular inversions which they carry, the chances of a tetraploid with 4 homologous chromosomes being heterozygous for any given inversion is materially increased.

More than one bridge has not been observed in the same cell, which might suggest that but a single inversion is involved in all of the plants. However, the frequency of bridges is so low that the chances of observing two bridges in a single cell from crossing over in two inversions would be very small indeed.

All of the species in which inversion bridges have been found are interfertile to some extent, and several of them grow in close proximity to one another or even together. The inversion heterozygotes referred to may therefore be the result of interspecific hybridization.

GEOGRAPHICAL DISTRIBUTION

The geographical distribution of the colonies in which chromosome counts were made, including their precise locations, are indicated in the following list, together with label data which will identify the vouchers on file in the herbarium of the University of California, Los Angeles. The number of plants at each locality of which the chromosome number was determined is shown in parentheses. In some cases two collections from the same colony are combined. The species concerned are listed alphabetically.

DELPHINIUM ANDERSONI Gray ($2n = 16$)

LASSEN CO.: 3.3 mi. n. of Ravendale, *Mehlquist & Jenkins* 380 (3).

MODOC CO.: west cinder-slope of Sconchin Butte, Lava Beds Nat'l. Mon., *Mehlquist & Jenkins* 377 (3); n. base of Caldwell Butte, Lava Beds Nat'l. Mon., *Mehlquist & Jenkins* 378 (2).

DELPHINIUM CALIFORNICUM T. & G. ($2n = 16$)

CONTRA COSTA CO.: near Juniper Camp, Mt. Diablo, *Mehlquist & Compton* 305 (5). MONTEREY CO.: near Aromas, *Mehlquist* 300 (5).

DELPHINIUM CARDINALE Hook. ($2n = 16$)

LOS ANGELES CO.: Sepulveda Canyon, Santa Monica Mts., *Mehlquist & Compton* 301 (6); San Antonio Wash near Claremont, *Mehlquist & Compton* 296 (5).

SAN BERNARDINO CO.: 2 mi. e. of Upland on Highland Ave., *Mehlquist* 396 (11).

SAN DIEGO CO.: near Banner, *Mehlquist & Geissman* 404 (4).

SANTA BARBARA CO.: near Lompoc, *Mehlquist* 20 (5); 3 mi. s. of Lompoc on the Santa Rosa Rd., *Mehlquist* 295 (yellow-flowered) (5).

DELPHINIUM DECORUM Fisch. & Mey. subsp. TRACYI Ewan ($2n = 16$)

HUMBOLDT CO.: 2 mi. s. of Kneeland on the rd. to Bridgeville, *Mehlquist & Jenkins* 368 (4); South Fork of Van Duzen R., *Mehlquist & Jenkins* 374 (4).

DELPHINIUM GLAUCUM Wats. ($2n = 16$)

SAN BERNARDINO CO.: Dobb's Cabin, San Bernardino Mts., *Mehlquist & Compton* 302 (6).

DELPHINIUM GRACILENTUM Greene ($2n = 16$)

BUTTE CO.: 2.5 mi. n. of Little Butte Creek bridge on the Paradise to De Sabla Rd., May 25, 1941, *Lewis & Epling* (1).

DELPHINIUM GYPSOPHILUM Ewan, *Diploid* ($2n = 16$) (Fig. 2)

KERN CO.: 1 mi. s. w. of Poso Creek on the Bakersfield to Woody Rd., April 14, 1944, *Lewis & Epling* (15); U. S. Hwy. 466, 4.2 mi. n. of the w. rd. to Caliente, April 22, 1943, *Lewis & Epling* (15); 1.5 mi. n. of McKittrick on Hwy. 33, *Mehlquist* 411, April 23, 1943, *Lewis & Epling* (19); 5.0 mi. s. w. of Maricopa on U. S. Hwy. 399, *Lewis & Epling* 531, *Epling & Miles* 545 (47).

MONTEREY CO.: 2.4 mi. w. of the jtn. at Pleyto, *Lewis & Epling* 697 (1); 3.0 mi. w. of the jtn. at Pleyto, *Lewis & Epling* 657, 699 (1); 4 mi. w. of the jtn. at Pleyto, *Lewis & Epling* 698 (8); 6.2 mi. e. of King City on the rd. to Hollister, *Lewis & Mehlquist* 431 (1); Bradley to Jolon rd. at jtn. with rd. to Pleyto, *Lewis & Epling* 694, 782 (9).

SAN BENITO CO.: 0.8 mi. w. of Bitterwater, *Lewis & Epling* 820 (1).

SAN LUIS OBISPO CO.: 2.9 mi. w. of U. S. Hwy. 101 on rd. to Cambria from Templeton, *Lewis & Epling* 664 (4); 1.5 mi. s. of Klau, *Lewis & Epling* 661, 689 (13); 0.6 mi. w. of Hwy. 41 on the Hillman to Estrella rd., *Epling* 735 (6); 6.1 mi. s. of U. S. Hwy. 466 on the rd. to Simmler, *Lewis & Epling* 715 (3); near Adelaida, *Lewis & Epling* 692 (9).

DELPHINIUM GYPSOPHILUM Ewan, *Tetraploid* ($2n = 32$) (Fig. 2)

FRESNO CO.: 5.5 mi. n. of Coalinga on Hwy. 33, *Lewis & Mehlquist* 451 (3); 7.2 mi. n. of Coalinga on Hwy. 33, *Lewis & Epling* 537, *Lewis & Mehlquist* 455 (9); 13.6 mi. n. of Coalinga on Hwy. 33, *Mehlquist* 414, *Lewis & Mehlquist* 454 (5); 14.9 mi. n. of Coalinga on Hwy. 33, *Lewis & Epling* 530 (38); 5.2 mi. w. of Coalinga on Hwy. 198, *Lewis & Mehlquist* 441 (48).

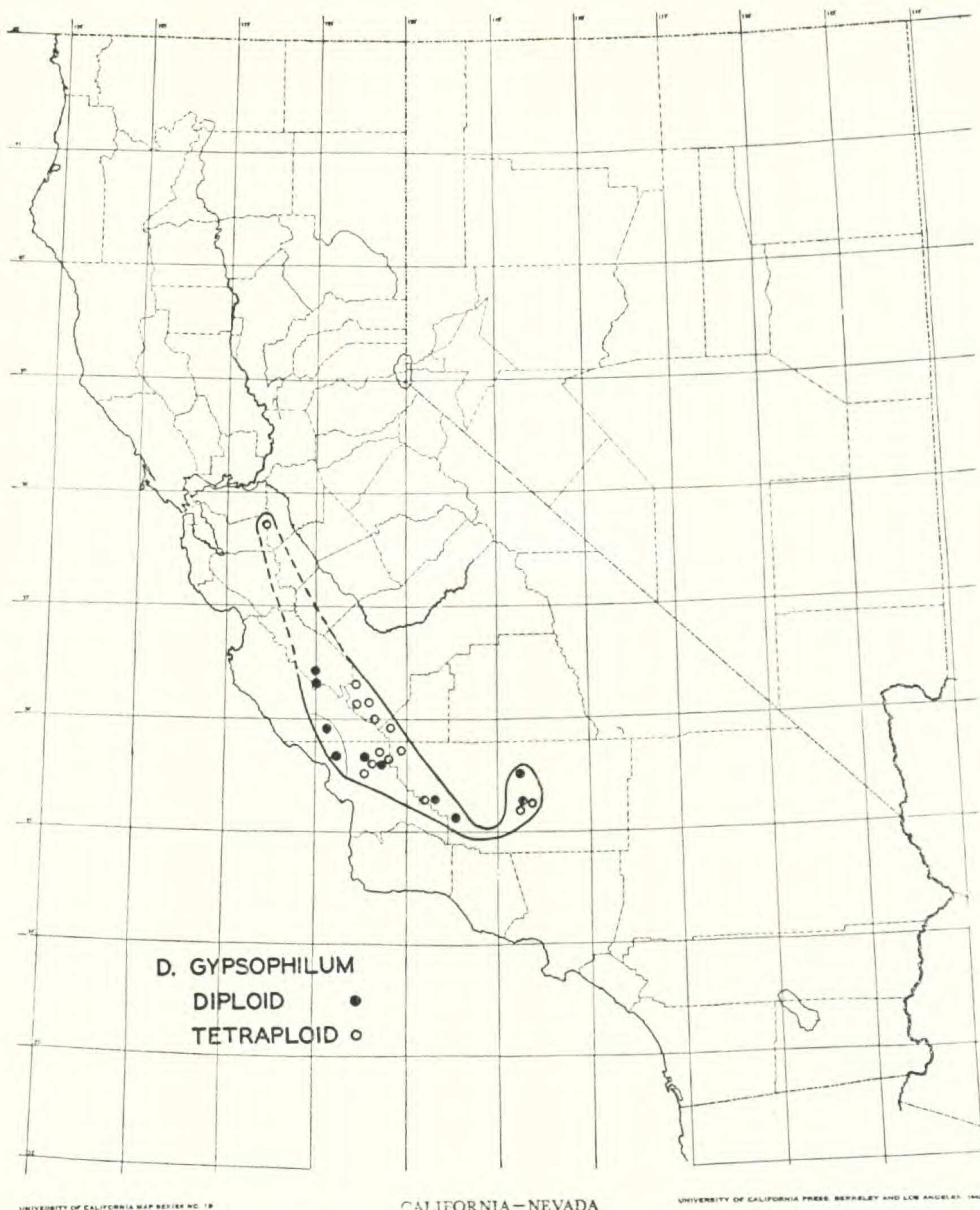


Fig. 2. Distribution of *D. gypsophilum* showing stations from which plants have been examined cytologically.

KERN CO.: about 2 mi. e. of McKittrick, Mehlquist & Wyckoff 332 (4); 8.7 mi. w. of McKittrick, Apr. 23, 1943, Lewis & Epling (25); Cottonwood Pass on Hwy. 41, 0.6 mi. e. of the San Luis Obispo Co. line, Apr. 24, 1943, Lewis & Epling (13); 0.4 mi. e. of Caliente R. R. Station, Lewis & Epling 493 (5); 1 mi. w. of Caliente R. R. Station, Lewis & Epling 494, Epling 585 (20); 4.2 mi. w. of Caliente R. R. Station, Apr. 22, 1943, Lewis & Epling (6); U. S. Hwy. 466, 0.4 mi. n. of the w. rd. to Caliente, Apr. 22, 1943, Lewis & Epling (6); U. S. Hwy. 466, 0.9 mi. n. of the w. rd. to Caliente, Apr. 22, 1943, Lewis & Epling (4); U. S. Hwy. 466, 1.0 mi. n. of the w. rd. to Caliente, Lewis & Epling 529 (10); U. S. Hwy. 466, 2.9 mi. n. of the w. rd. to Caliente, Apr. 22, 1943, Lewis &

Epling (3); U. S. Hwy. 466, 3.0 mi. n. of the w. rd. to Caliente, Apr. 22, 1943, *Lewis & Epling* (12); U. S. Hwy. 466, 4.2 mi. n. of the w. rd. to Caliente, *Lewis, Epling & Mehlquist* 458 (9).

KINGS CO.: hills e. of Avenal, *Mehlquist & Blodgett* 331 (6).

SAN JOAQUIN CO.: 1 mi. e. of Midway, *Lewis & Mehlquist* 452, *Epling & Miles* 543 (4).

SAN LUIS OBISPO CO.: 2.8 mi. e. of the jtn. of U. S. Hwy. 466 and Hwy. 41 near Cholame, Apr. 24, 1943, *Lewis & Epling* (31); U. S. Hwy. 466, 1.4 mi. e. of jtn. of Hwy. 41 near Cholame, *Lewis & Epling* 713 (9); 6.1 mi. s. of U. S. Hwy. 466 on the rd. to Simmler, *Lewis & Epling* 715 (1); 5.1 mi. n. e. of Creston on the rd. to Shandon, *Lewis* 816 (1); 5.2 mi. s. w. of U. S. Hwy. 41 on the Shandon to Creston rd., *Lewis & Epling* 821 (1).

DELPHINIUM HANSENI Greene, *Diploid* ($2n = 16$) (Fig. 3)

AMADOR CO.: 2.6 mi. n. of Jackson, May 20, 1945, *Epling* (1); 3.5 mi. s. of Jackson on Hwy. 49, *Epling* 584 (3); 3.7 mi. s. of Jackson on Hwy. 49, May 20, 1945, *Epling* (6).

BUTTE CO.: 2.5 mi. e. of Oroville city limits, *Epling* 666 (1).

CONTRA COSTA CO.: Marsh Creek Rd., 5.8 mi. e. of the Curry Creek Park Rd., *Lewis & Epling* 703 (3).

ELDORADO CO.: 0.5 mi. w. of Garden Valley, May 26, 1941, *Lewis & Epling* (1).

KERN CO.: 10 mi. e. of Hwy. 65 on the rd. to Woody, *Epling* 560 (1); 1.9 mi. sw. of Woody, *Mehlquist* 338 (1); 3.1 mi. s. w. of Woody, May 18, 1945, *Epling* (9); 3.6 mi. s. w. of Woody, *Lewis & Epling* 528 (9); 5.3 mi. s. w. of Woody, May 18, 1945, *Epling* (7); 5.5 mi. s. w. of Woody, May 18, 1945, *Epling* (5); 3.7 mi. s. of White River, *Epling* 561 (6); Glennville Church, *Mehlquist & Wyckoff* 327 (3); 1.2 mi. e. of Glennville, *Lewis, Epling & Mehlquist* 469 (5); 2 mi. e. of Onyx, *Lewis & Epling* 484 (16); 3.7 mi. e. of mouth of Kern River Canyon, *Mehlquist & Wyckoff* 323 (3); about 5 mi. e. of the mouth of the Kern River Canyon, *Mehlquist & Wyckoff* 322 (3); 6.1 mi. e. of the mouth of the Kern River, *Mehlquist* 337, *Lewis & Mehlquist* 465 (6); 1.0 mi. w. of Bodfish, Apr. 30, 1946, *Lewis & Epling* (1); 3.6 mi. s. of Bodfish, *Lewis & Epling* 485 (16); 10.1 mi. s. of Bodfish, *Lewis & Epling* 487 (16); 12.5 mi. s. of Bodfish, May 24, 1943, *Lewis, Epling & Mehlquist* (13); 1.3 mi. e. of the cemetery, Walker Basin, *Lewis & Epling* 488 (30); Oiler Canyon Rd., 3.5 mi. s. of the jtn. at the s. w. margin of Walker Basin, *Lewis & Epling* 489 (14); Oiler Canyon Rd., 6.5 mi. s. of the jtn. at the s. w. margin of Walker Basin, *Lewis & Epling* 490 (3); Oiler Canyon Rd., 8.5 mi. s. of the jtn. at the s. w. margin of Walker Basin, *Lewis & Epling* 492 (20); 1 mi. w. of Caliente R. R. Station, Apr. 22, 1943, *Lewis & Epling* (1); 3.5 mi. w. of Caliente R. R. Station, *Lewis & Epling* 495 (19); 1.8 mi. e. of U. S. Hwy. 466 on the w. rd. to Caliente, *Mehlquist & Lewis* 437, *Lewis, Epling & Mehlquist* 457 (8); U. S. Hwy. 466, 0.4 mi. n. of the w. rd. to Caliente, Apr. 22, 1943, *Lewis & Epling* (1); U. S. Hwy. 466, 0.6 mi. n. of the w. rd. to Caliente, *Lewis & Epling* 496 (7); U. S. Hwy. 466, 1.5 mi. n. of the w. rd. to Caliente, *Epling* 559, Apr. 22, 1943, *Lewis & Epling* (31); U. S. Hwy. 466, 1.8 mi. n. of the w. rd. to Caliente, Apr. 22, 1943, *Lewis & Epling* (7); U. S. Hwy. 466, 2.0 mi. n. of the w. rd. to Caliente, Apr. 22, 1943, *Lewis & Epling* (3); U. S. Hwy. 466, 2.3 mi. n. of the w. rd. to Caliente, Apr. 22, 1943, *Lewis & Epling* (4); U. S. Hwy. 466, 2.9 mi. n. of the w. rd. to Caliente, Apr. 22, 1943, *Lewis & Epling* (37); U. S. Hwy. 466, 3.0 mi. n. of the w. rd. to Caliente, Apr. 22, 1943, *Lewis & Epling* (3); U. S. Hwy. 466, 3.4 mi. n. of the w. rd. to Caliente, Apr. 22, 1943, *Lewis & Epling* (4); U. S. Hwy. 466, 3.8 mi. n. of the w. rd. to Caliente, Apr. 22, 1943, *Lewis & Epling* (4); U. S. Hwy. 466, 4.2 mi. n. of the w. rd. to Caliente, *Lewis, Epling & Mehlquist* 459, 461 (21); U. S. Hwy. 466, 4.1 mi. e. of the w. rd. to Caliente, *Lewis & Epling* 500 (13).

MADERA CO.: Madera to Raymond Rd., 1.1 mi. e. of the jtn. with the Chowchilla Rd., *Epling* 564 (4); Raymond to Coarsegold Rd., 4.9 mi. e. of the jtn. to Knowles, *Epling* 568 (1); 1.0 mi. s. of Raymond, *Epling* 567 (2); 1.4 mi. s. of Raymond, *Epling* 566 (3); 1.6 mi. s. of Raymond, *Epling* 565 (2).

MARIPOSA CO.: 6.8 mi. s. of Mariposa, *Mehlquist* 346 (4); Hwy. 140, 15 mi. e. of the rd. to LeGrand, *Epling* 570 (1); 8.1 mi. s. of Coulterville, *Mehlquist* 347 (3); Merced River, 1.3 mi. s. of El Portal, *Lewis* 761 (2).

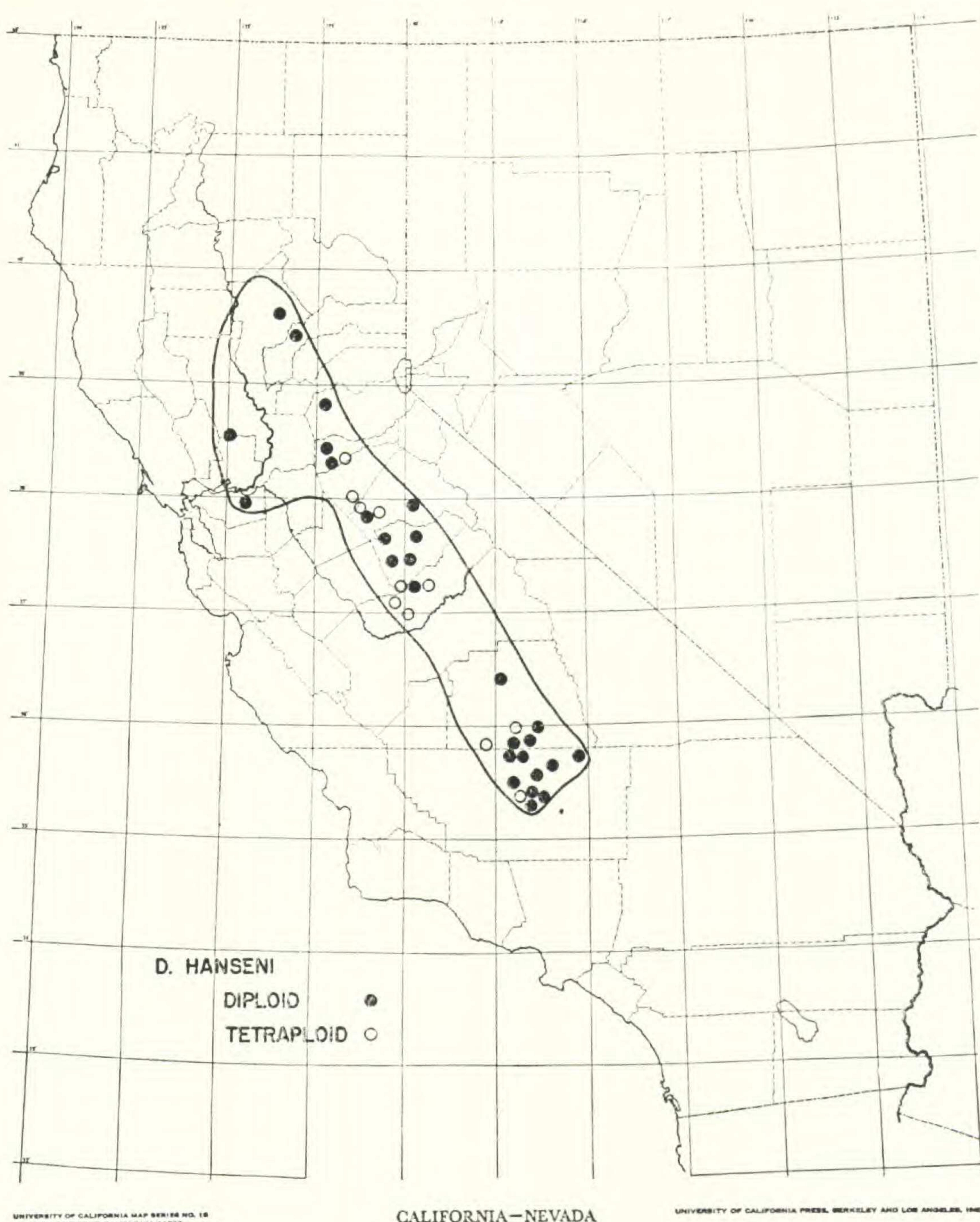


Fig. 3. Distribution of *D. hansenii* showing stations from which plants have been examined cytologically.

TULARE CO.: Kern River near Durrwood, Lewis, Epling & Mehlquist 509 (5); Kern River at Welch (near Fairview), May 24, 1943, Lewis, Epling & Mehlquist (2); 1.9 mi. e. of Lemon Cove, May 18, 1945, Epling (2); 4.2 mi. e. of Lemon Cove, Epling 563 (5); 0.3 mi. n. of White River, Lewis, Epling & Mehlquist 470 (1); 0.7 mi. n. of White River, Lewis, Epling & Mehlquist 472 (2); 1.0 mi. n. of White River, Mehlquist & Wyckoff 329 (2); about 1.5 mi. n. of White River, Mehlquist & Wyckoff 330 (3); 1.9 mi. n. of White River, May 18, 1945, Epling (4); 2.6 mi. n. of White River, Lewis, Epling & Mehlquist 473 (1).

TUOLUMNE CO.: 4.8 mi. e. of Mather Ranger Station, *Epling* 770 (6); 5.9 mi. e. of Mather Ranger Station, *Epling* 771 (4); Jacksonville, 0.6 mi. w. of the jtn. of Hwy. 49 and Hwy. 120, *Epling* 579 (2).

YOLO CO.: 3.8 mi. w. of Winters, *Mehlquist & Baker* 314, *Lewis & Epling* 606 (5).

YUBA CO.: 3.4 mi. e. of Oregon House P. O., *Lewis* 764 (3).

DELPHINIUM HANSENI Greene, *Tetraploid* ($2n = 32$) (Fig. 3)

AMADOR CO.: 2.6 mi. n. of Jackson, May 20, 1945, *Epling* (4).

CALAVERAS CO.: 1.6 mi. n. of Copperopolis Ranger Station on Hwy. 4, *Epling* 582 (4); 4.5 mi. n. of Hwy. 120 on the rd. to Copperopolis, *Epling* 581 (4).

KERN CO.: U. S. Hwy. 466, 4.2 mi. n. of the w. rd. to Caliente, *Mehlquist & Lewis* 425, 426, 427, 460 (81).

MADERA CO.: Coarsegold to Madera Rd., 0.6 mi. s. of Raymond Rd., *Epling* 569 (2); Madera to Raymond Rd., 1.1 mi. e. of jtn. with Chowchilla Rd., *Epling* 564 (2); 1.7 mi. n. of the viaduct over the Fresno River at Madera, *Epling & Miles* 544 (1); 4.7 mi. n. of Madera, *Mehlquist* 345A (5); 5 mi. n. of Madera, *Lewis & Mehlquist* 438 (3); 10 mi. n. of Madera, *Lewis & Mehlquist* 432, 433 (4); 13 mi. n. of Madera, *Mehlquist* 345B (3).

TULARE CO.: 1.6 mi. n.e. of Richgrove, *Lewis, Mehlquist* 475, *Epling & Miles* 540 (1); 0.7 mi. n. of White River, *Mehlquist & Wyckoff* 328, *Lewis, Epling & Mehlquist* 471 (20); 2.6 mi. n. of White River, *Lewis, Epling & Mehlquist* 474 (4).

TUOLUMNE CO.: Jacksonville, 0.6 mi. w. of the jtn. of Hwy. 49 and Hwy. 120, *Epling* 578 (4); 0.5 mi. n.w. of Jamestown on the Tuttletown Rd., *Epling* 723 (1).

DELPHINIUM HESPERIUM Gray ($2n = 16$) (Fig. 4)

LAKE CO.: 5 mi. e. of the Lake Co. line on the Lakeport to Hopland Rd., *Lewis, Epling & Stebbins* 516 (4).

MENDOCINO CO.: 9.6 mi. s. of Rock Creek, *Mehlquist & Jenkins* 366 (2).

NAPA CO.: 6 mi. s. of Monticello on the rd. to Napa, *Mehlquist* 355 (3); 6.8 mi. s. of Monticello on the rd. to Napa, *Mehlquist & Paddock* 308, *Mehlquist* 356 (4); 7 mi. s. of Monticello on the rd. to Napa, *Mehlquist* 357 (2); 8.4 mi. s. of Monticello on the rd. to Napa, *Mehlquist* 358 (2); Wooden Valley, *Mehlquist* 400 (1).

SAN MATEO CO.: Page Mill Rd., near Stanford Univ., *Lewis & Epling* 436 (3).

SANTA CLARA CO.: Uvas Creek, *Lewis & Epling* 435 (2).

SONOMA CO.: 1 mi. e. of Bodega Bay, *Lewis & Epling* 515 (2); Mark West Springs, *Mehlquist & Jenkins* 362 (5).

DELPHINIUM HESPERIUM Gray forma PALLESCENS Ewan ($2n = 16$) (Fig. 4)

This entity, described by Ewan (1945) as *D. hesperium* forma *pallescens*, is most conspicuously distinguished from the typical form by its white or pinkish flowers and is a readily recognized geographical race of the drier more interior foothills of the Coast Ranges (fig. 4). In our opinion it unquestionably warrants subspecific status. The combination required will be made in another publication.

CONTRA COSTA CO.: Marsh Creek Rd., 1 mi. w. of Curry Creek Park Rd., *Lewis & Epling* 702 (1); rd. to Livermore, 0.1 mi. s. of the Marsh Creek Rd., *Lewis & Mehlquist* 444 (3); Beck Rd. (to Livermore), 1.0 mi. s. of the Marsh Creek Rd., *Lewis & Epling* 589 (22); Beck Rd. (to Livermore), 1.2 mi. s. of the Marsh Creek Rd., May 6, 1944, *Lewis & Epling* (5); rd. to Antioch, 4.5 mi. n. of the Marsh Creek Rd., *Lewis & Mehlquist* 446 (5); Antioch Golf Course, *Lewis & Mehlquist* 445 (5).

LAKE CO.: 2.7 mi. n. of Clear Lake on rd. to Stubbs, *Mehlquist & Jenkins* 364 (1).

NAPA CO.: 2 mi. n. of Knoxville on the rd. to Reiff, *Mehlquist & Paddock* 309, *Mehlquist & Baker* 319 (5); 4.6 mi. s. of Monticello on Napa Rd., *Mehlquist* 354 (3).

SAN BENITO CO.: 0.5 mi. s. of Paicines, *Lewis & Mehlquist* 450 (4); 2.8 mi. s. of the entrance to the Pinnacles, *Lewis & Mehlquist* 449 (3); 4.1 mi. s. of Pinnacles P. O., *Mehlquist* 386 (6); 9.9 mi. s. of Paicines, *Lewis & Epling* 709 (4).

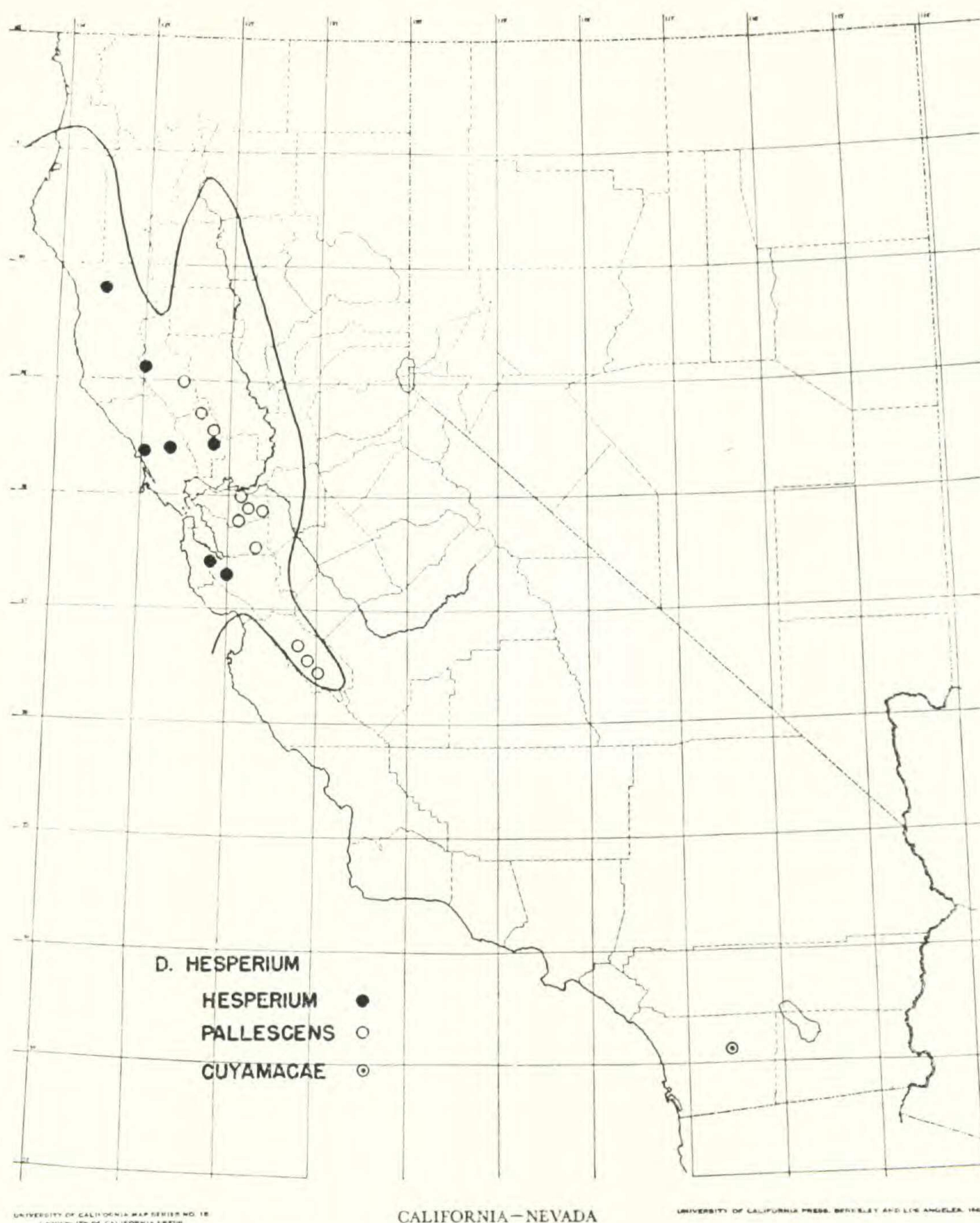


Fig. 4. Distribution of *D. hesperium* showing stations from which plants have been examined cytologically.

YOLO CO.: Putah Creek Canyon, 8 mi. w. of Winters, Mehlquist & Baker 315 (4).

DELPHINIUM HESPERIUM Gray var. CUYAMACAE (Abrams) Jeps. ($2n = 16$) (Fig. 4)

SAN DIEGO CO.: Cuyamaca Lake, Mehlquist & Geissman 403, Ensign & McClintock 554 (9).

DELPHINIUM INOPINUM ($2n = 16$)

We have evidence to indicate that *D. parishii* var. *inopinum* Jeps. represents a good species. The new combination required will be made elsewhere.

VENTURA CO.: 1.0 mi. w. of Chuchupate Ranger Station, *Ball* 807, *Lewis* 630 (3); 13.2 mi. s. of Ozena on U. S. Hwy. 399, *Lewis & Epling* 755 (1); 13.6 mi. s. of Ozena on U. S. Hwy. 399, *Lewis & Epling* 756 (2).

DELPHINIUM NUDICAULE T. & G. ($2n = 16$)

HUMBOLDT CO.: S. Fork Van Duzen Rd., *Mehlquist & Jenkins* 375 (3).

MODOC CO.: s. slope of Caldwell Butte, Lava Beds Nat'l. Mon., *Mehlquist & Jenkins* 379 (5).

NAPA CO.: 12 mi. n. of Monticello on rd. to Knoxville, *Mehlquist & Baker* 318 (3); 11 mi. n. of Monticello on rd. to Knoxville, *Mehlquist* 350 (3); 16.5 mi. s. of Monticello on rd. to Napa, *Mehlquist* 359 (4); Nuns Canyon, *Mehlquist & Baker* 321, *Mehlquist & Jenkins* 361 (5).

SANTA CRUZ CO.: 0.9 mi. n. of Brookdale Resort, Santa Cruz Mts., *Mehlquist* 333 (3).

DELPHINIUM NUTTALLIANUM Pritz. ($2n = 16$)

NEVADA CO.: Soda Springs Hotel, *Mehlquist & Jenkins* 381 (5).

DELPHINIUM PARISHII Gray ($2n = 16$) (Fig. 5)

INYO CO.: Westgaard Pass, *Bobart* 419 (1); Canyon near Hells Gate, Death Valley Nat'l. Mon., *Lewis & Lowe* 682 (3); Emigrant Canyon, Death Valley Nat'l. Mon., *Lewis & Lowe* 681 (4).

KERN CO.: road to Cuddy Valley, 0.1 mi. n. of the Cuyama Valley Rd., *Lewis & Dunn* 478 (6); 1.0 mi. w. of Chuchupate Ranger Station, *Lewis* 749 (1); 1 mi. e. of the summit of Walker Pass, *Lewis, Epling & Mehlquist* 467 (2); Summit of Walker Pass, *Lewis, Epling & Mehlquist* 466 (2); 7.1 mi. w. of the summit of Walker Pass, *Lewis, Epling & Mehlquist* 468 (1).

LOS ANGELES CO.: Palmdale, *Epling* 745 (2); 23.5 mi. e. of Palmdale, Apr. 17, 1941, *Lewis & Epling* (1); near Lancaster, *Mehlquist* (5).

RIVERSIDE CO.: Palm Springs, mouth of Tahquitz Canyon, *Lewis* 811 (1).

SAN BERNARDINO CO.: 4.9 mi. n. of the jtn. of the Mojave River and Deep Creek, Apr. 25, 1941, *Lewis & Epling* (1); Morongo Valley, Apr. 27, 1941, *Lewis & Epling* (1); grade between Morongo Valley and Yucca Valley, *Mehlquist* 333, *Lewis & Epling* 508 (15); 4.8 mi. s. of Barstow on the rd. to Stoddard Well, Apr. 27, 1941, *Lewis & Epling* (1); 8.2 mi. s. of Barstow on the rd. to Stoddard Well, Apr. 27, 1941, *Lewis & Epling* (1); the Mojave River Narrows at Victorville, Apr. 27, 1941, *Lewis & Epling* (1); near Baldwin Lake, *Mehlquist* 421, 422, 424 (6); Holcomb Valley, *Mehlquist* 420 (1); Avawatz Mts., C. Wolf (*Mehlquist* 303) (1).

SAN DIEGO CO.: 1.2 mi. w. of bridge in Sentenac Canyon, *Mehlquist & Geissman* 407 (2); 2.4 mi. w. of bridge, *Mehlquist & Geissman* 408 (2); mouth of Coyote Canyon, *Mehlquist & Geissman* 409 (2); mouth of Borego Palm Canyon, *Mehlquist & Geissman* 410 (2).

DELPHINIUM PARRYI Gray ($2n = 16$) (Fig. 5)

INYO CO.: Sherman Hills above Paradise Camp, n. of Bishop, *Bobart* 419 (2).

LOS ANGELES CO.: Santa Catalina Island, west end of Whitley Ave., Avalon, *Lewis* 631 (1); Mulholland Drive e. of Topanga Canyon Rd., *Mehlquist & Wyckoff* 391, 392 (5); Lopez Canyon, *Mehlquist* 312, 40016 (9).

MONTEREY CO.: 1.0 mi. w. of the jtn. at Pleyto, *Lewis & Epling* 695 (4); 1.5 mi. w. of the jtn. at Pleyto, *Lewis & Epling* 696 (2); Bradley to Jolon Rd., at jtn. with Pleyto Rd., *Levine* 774 (1).

RIVERSIDE CO.: Santa Rosa Summit, *Lewis & Epling* 482 (1); 3 mi. s. of Banning on the rd. to Idyllwild, *Mehlquist* 334 (3).

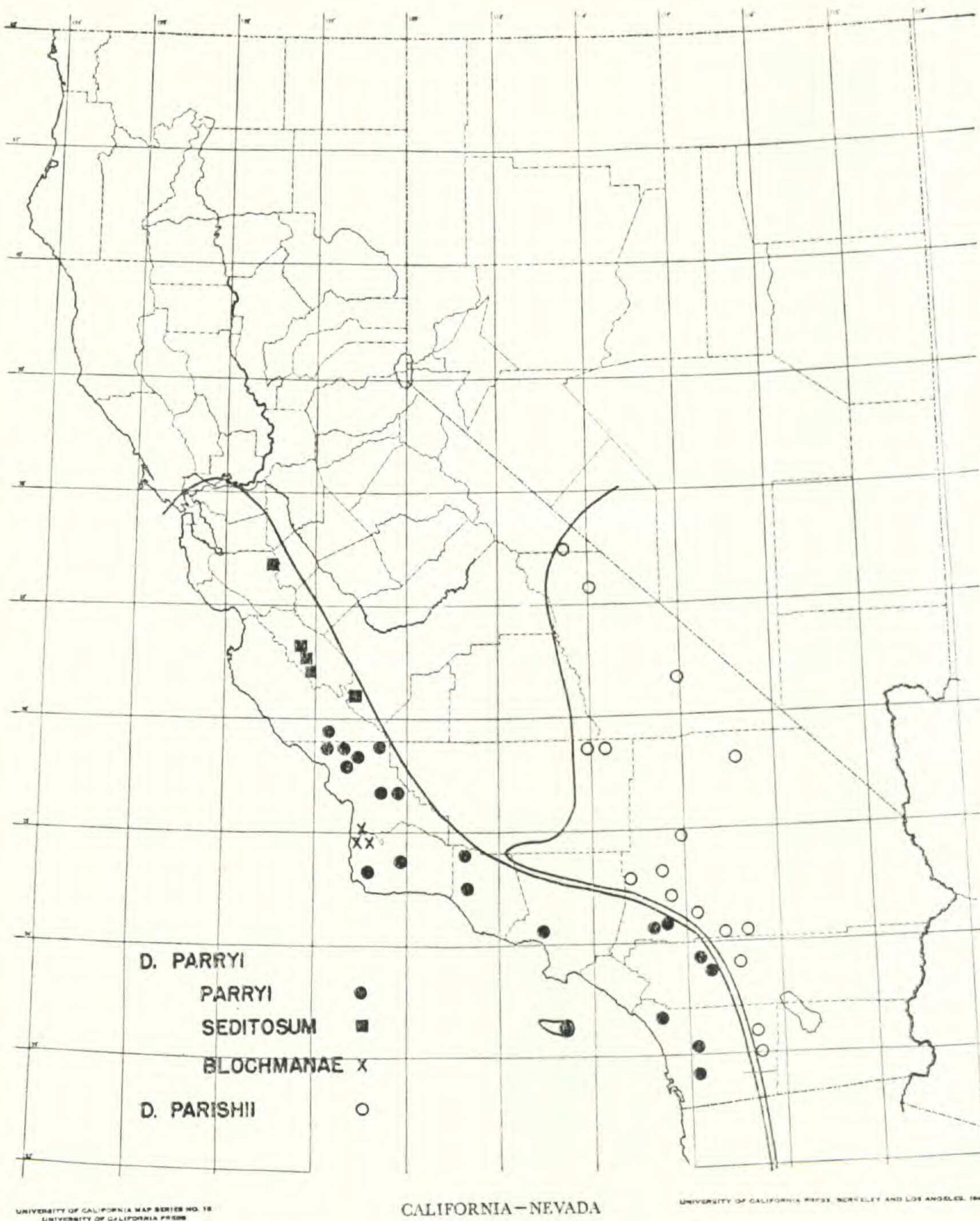


Fig. 5. Distribution of *D. parryi* and *D. parishii* showing stations from which plants have been examined cytologically.

SAN BERNARDINO CO.: Cedar Springs, *Lewis & Epling* 534 (1); 5 mi. n. of Verdemont, Apr. 1944, *Lewis* (1); near the Zanja, Mentone, Apr. 20, 1946, *Lewis* (1).

SAN DIEGO CO.: Lakeside Park, *Froelich* 313 (4); Ramona, *Mehlquist* 307 (4); near Fallbrook, *Mehlquist & Eggers* 393 (2).

SAN LUIS OBISPO CO.: 1.9 mi. w. of Pozo, May 24, 1941, *Lewis & Epling* (1); 6.1 mi. s. of U. S. Hwy. 466 on rd. to Simmler, *Lewis & Epling* 714 (2); 7.1 mi. w. of Simmler, *Lewis & Epling* 501 (7); 4.1 mi. s. and 1.1 mi. e. of Atascadero, *Dunn & Brown* 2383 (1); 1.5 mi. s. of Klau, *Lewis & Epling* 662 (3); 8.5 mi. n.w. of Adelaida Cemetery, *Lewis & Epling* 659 (2); 9.3 mi. n.w. of Adelaida Cemetery, *Lewis & Epling* 658 (3); 9.9

mi. w. of U. S. Hwy. 101 on the n. rd. to Adelaida, *Lewis & Epling* 687 (2); 3.5 mi. e. of Santa Margarita on the rd. to Creston, *Lewis & Epling* 653 (2); Santa Margarita, *Mehlquist* 389 (5); rd to Creston, 4.2 mi. n. of Santa Margarita to Pozo Rd., *Ball* 802 (3).

SANTA BARBARA CO.: Davy Brown Camp, Figueroa Mt., *Epling* 477 (12); 0.8 mi. s. of Davy Brown Camp, Figueroa Mt., *Lewis* 720 (7); 1.1 mi. n. of Red Rock Mine on the Santa Inez Valley to Davy Brown Rd., *Lewis* 722 (3); Lompoc, *Mehlquist* 399, 481 (3).

VENTURA CO.: Ojai, 1942, *Mehlquist* (1); U. S. Hwy. 399, 9 mi. s. of jtn. with Mt. Pinos Rd., *Lewis & Epling* 754 (6).

DELPHINIUM PARRYI ssp. *SESTITIOSUM* (Jeps.) Ewan ($2n = 16$) (Fig. 5)

FRESNO CO.: 6 mi. w. of Coalinga, *Lewis & Mehlquist* 434 (2); 7.6 mi. w. of jtn. of the Los Gatos Creek Rd. and the rd. to Coalinga, *Lewis & Epling* 628 (1); 10.9 mi. w. of jtn. of the Los Gatos Creek Rd. and the rd. to Coalinga, *Lewis & Epling* 624 (1).

SAN BENITO CO.: 0.4 mi. n. of the entrance to the Pinnacles, *Lewis & Mehlquist* 456 (2); 9.4 mi. s. of Pinnacles P. O., *Mehlquist* 388 (4); 2.9 mi. n. of Pinnacles P. O., *Mehlquist* 385 (2); 6.7 mi. n. of Pinnacles P. O., *Mehlquist* 384 (3); 5.1 mi. s. of Pinnacles P. O., *Mehlquist* 387 (2).

SANTA CLARA CO.: Livermore-Mt. Hamilton Rd., 0.9 mi. n. of Del Puerto Rd. to Patterson, *Lewis & Epling* 610 (2); Livermore-Mt. Hamilton Rd., 1.8 mi. n. of Del Puerto Rd. to Patterson, *Lewis & Epling* 609 (1); Livermore-Mt. Hamilton Rd., 1.3 mi. s. of Del Puerto Rd. to Patterson, *Lewis & Epling* 615 (1).

DELPHINIUM PARRYI Gray var. *BLOCHMANAE* (Greene) Jeps. ($2n = 16$) (Fig. 5)

SAN LUIS OBISPO CO.: 5.5 mi. n. of Guadalupe, *Mehlquist* 513 (3); dunes to the w. of the Nipomo to Guadalupe Rd., *Lewis & Epling* 504 (9); 5.3 mi. n. of Veterans Memorial in Guadalupe, *Lewis & Epling* 685 (4); U. S. Hwy. 101, 11.1 mi. n. of Los Alamos, *Lewis & Epling* 505 (8).

DELPHINIUM PATENS Benth. ($2n = 16$)

KERN CO.: 6.5 mi. s. of Walker Basin on the Oiler Canyon Rd., *Lewis & Epling* 491 (1); Kern River Canyon, about 5 mi. e. of mouth, *Mehlquist & Wyckoff* 326 (3).

LOS ANGELES CO.: Pacoima Canyon, San Gabriel Mts., *Mehlquist & Froelich* 306 (5); near Mt. Wilson Toll Rd., *Mehlquist* 398 (2).

MONTEREY CO.: near Priest Valley, *Mehlquist* 298 (2); near Aromas, *Mehlquist* 299 (2).

NAPA CO.: 11 mi. n. of Monticello, on the rd. to Knoxville, *Mehlquist* 316A (1).

RIVERSIDE CO.: about 15 mi. s. of Banning on the Idyllwild Rd., *Mehlquist* 335 (5).

SAN DIEGO CO.: Banner Grade, *Mehlquist & Geissman* 405 (3); 406 (2).

SANTA BARBARA CO.: San Marcos Pass Rd., 5 mi. n. of San Marcos Ranch, *Mehlquist* 390 (3).

VENTURA CO.: Mt. Pinos Public Camp, *Lewis & Dunn* 480 (1).

DELPHINIUM POLYCLADON Eastw. ($2n = 16$)

MARIPOSA CO.: e. end of Lake Tenaya, Aug. 22, 1941, *Lewis* (1).

DELPHINIUM PURPURUS Brandg. ($2n = 16$)

KERN CO.: about 2 mi. e. of the mouth of the Kern River Canyon, *Mehlquist & Wyckoff* 324 (3); 5.0 mi. e. of the mouth, *Lewis, Epling & Mehlquist* 464 (1); 3.7 mi. e. of the mouth, *Mehlquist* 336 (5).

DELPHINIUM RECURVATUM Greene ($2n = 16$)

CONTRA COSTA CO.: 0.5 mi. w. of Hwy. 120 on the Byron Hot Springs Rd., *Epling & Miles* 542 (3).

FRESNO CO.: 7.2 mi. n. of Coalinga on Hwy. 33, *Mehlquist* 412 (3); 13.6 mi. n. of Coalinga on Hwy. 33, *Mehlquist* 413, *Lewis & Mehlquist* 453 (11).

DELPHINIUM TROLLIIFOLIUM Gray ($2n = 16$)

HUMBOLDT CO.: 1.5 mi. n. of Kneeland, *Mehlquist & Jenkins* 367 (3); Yager Creek, *Mehlquist & Jenkins* 370 (3); Yager Creek bridge, 8 mi. n. of Bridgeville, *Mehlquist & Jenkins* 371 (2); 16.2 mi. n. of Bridgeville, *Mehlquist & Jenkins* 372 (1); 1.1 mi. w. of South Fork Van Duzen Rd. on rd. to Dinsmore, *Mehlquist & Jenkins* 373 (1).

DELPHINIUM ULIGINOSUM Curran ($2n = 16$)

LAKE CO.: 2.7 mi. e. of Middletown on rd. to Lower Lake, *Mehlquist & Baker* 320, *Mehlquist & Jenkins* 363 (10).

DELPHINIUM UMBRACULORUM ($2n = 16$)

Delphinium umbraculorum is an undescribed species. A formal taxonomic description will be presented elsewhere.

SAN LUIS OBISPO CO.: 3.7–4.0 mi. s. of Klau, *Lewis & Epling* 663, 691 (3); King City to Jolon Rd., 1.2 mi. n. of Avila, *Lewis & Epling* 701, 781 (1); Santa Margarita–Pozo Rd., 10.6 mi. e. of rd. to Creston, *Lewis* 813 (1).

SANTA BARBARA CO.: San Rafael Mts., Davy Brown Camp Ground, *Lewis* 717 (3); 0.8 mi. n. of Davy Brown Camp Ground, *Lewis & Mathias* 791 (1); 1.4 mi. n. of Davy Brown Camp Ground, *Lewis* 718, *Lewis & Mathias* 792 (3); about 5 mi. w. of Las Cruces–Lompoc Rd. on the rd. to Jalama, *Mehlquist* 512 (2); 0.3 mi. w. of Las Cruces–Lompoc Rd. on rd. to Jalama, *Lewis* 767 (8).

DELPHINIUM VARIEGATUM T. & G., Diploid ($2n = 16$) (Fig. 6)

ALAMEDA CO.: 10.7 mi. s. of Livermore P. O. on the Tesla–Corral Hollow Rd., *Lewis & Epling* 608 (15).

CALAVERAS CO.: 7.8 mi. s. of Mokelumne Hill, *Epling* 583 (4); 4.5 mi. n. of Hwy. 120 on the rd. to Copperopolis, *Epling* 580 (1).

CONTRA COSTA CO.: rd. to Livermore, 0.1 mi. s. of the Marsh Creek Rd., *Lewis & Mehlquist* 443 (6); 1.0 mi. s. of the Marsh Creek Rd. on the Beck Rd. to Livermore, *Lewis & Epling* 589 (5).

LAKE CO.: Lake-Napa County line, rd. Knoxville to Reiff, *Mehlquist & Paddock* 311 (5).

MARIPOSA CO.: 3.8 mi. n. of Bagby, *Epling* 572 (3); Hwy. 140, 16 mi. e. of the rd. to Le Grand, *Epling* 571 (5).

MENDOCINO CO.: 5.2 mi. s. of Willits on U. S. Hwy. 101, *Mehlquist & Jenkins* 365 (2).

NAPA CO.: 16.2 mi. n. of Monticello, *Mehlquist & Baker* 318, *Mehlquist* 351 (9); 2 mi. n. of Knoxville, *Mehlquist & Paddock* 309 (5); 6.8 mi. n. of Monticello on rd. to Knoxville, *Mehlquist & Baker* 316 (3); 0.7 mi. s. of Nuns Canyon, *Mehlquist & Jenkins* 360 (3).

SAN LUIS OBISPO CO.: 2.9 mi. w. of Pozo, *Lewis & Epling* 502 (12); 7.8 mi. w. of Pozo, Apr. 24, 1943, *Lewis & Epling* (10); near Santa Margarita, *Lewis & Epling* 503 (6).

SANTA CLARA CO.: Mt. Hamilton, *Paddock* 402 (3); Livermore to Mt. Hamilton Rd., 0.2 mi. w. of Mines Rd., *Lewis & Epling* 611 (1); Livermore to Mt. Hamilton Rd. at jtn. with Del Puerto Rd. to Patterson, *Lewis & Epling* 613 (2).

TULARE CO.: Pleasant Valley (near Springville), *Lewis & Epling* 526 (1).

TUOLUMNE CO.: 5.5 mi. e. of Hangman's Tree, Bret Harte, *Epling* 730 (1); Hwy. 108 at jtn. with rd. to Soulsbyville, *Epling* 576 (3).

PLACER CO.: Weimar, *Mehlquist & Jenkins* 382 (5).

DELPHINIUM VARIEGATUM T. & G., Tetraploid ($2n = 32$) (Fig. 6)

ELDORADO CO.: 0.5 mi. w. of Garden Valley, *Lewis & Epling* 442 (2).

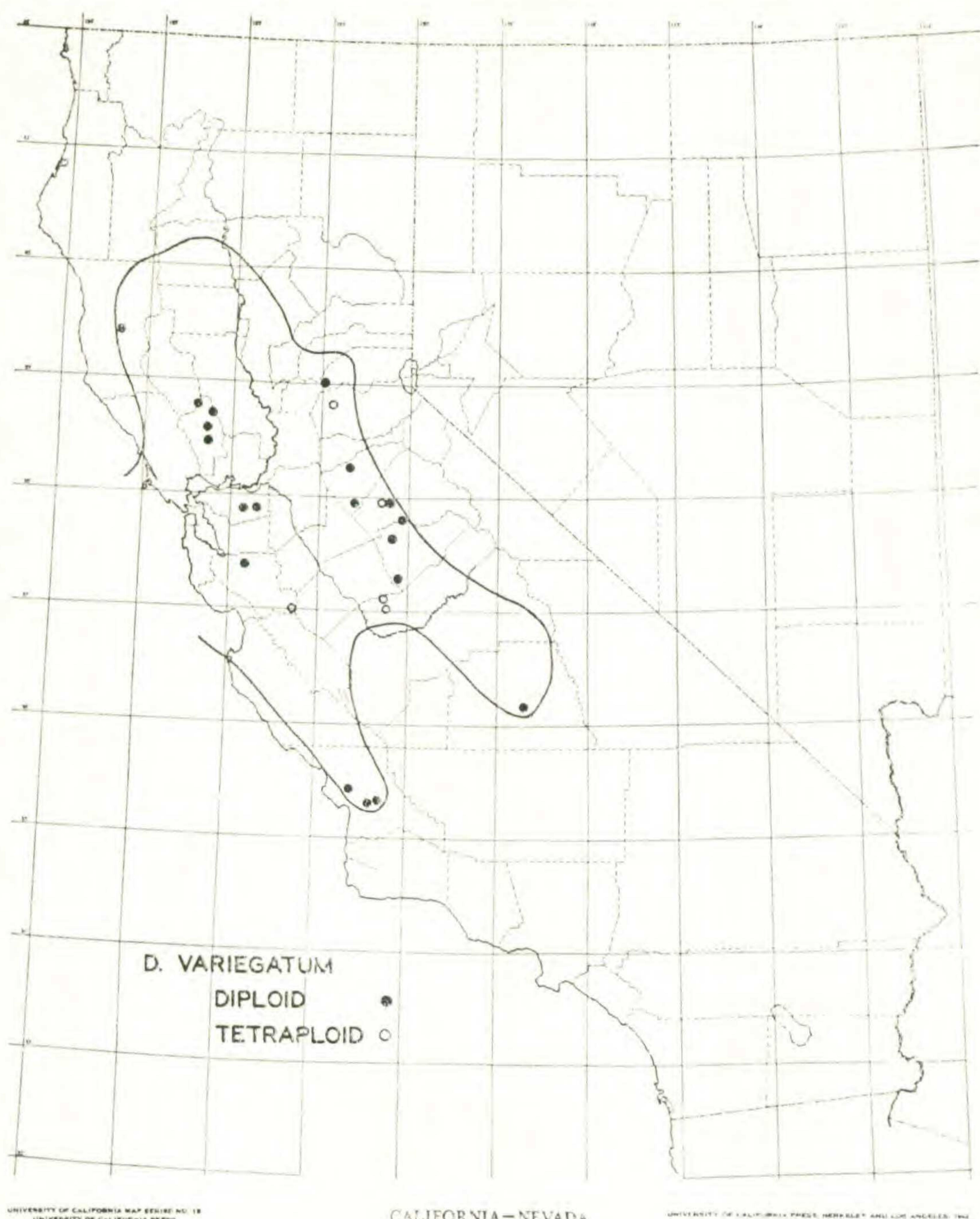


Fig. 6. Distribution of *D. variegatum* showing stations from which plants have been examined cytologically.

MADERA CO.: 0.5 mi. n. of the n. end of the bridge over the Fresno R. at Madera, Epling & Miles 541 (2); 10 mi. n. of Madera, Lewis & Mehlquist 433 (3); 21.8 mi. s. of Merced, Lewis & Mehlquist 447 (7).

MERCED CO.: Pacheco Pass, Mehlquist 416, 417 (9).

TUOLUMNE CO.: Hwy. 108, 0.7 mi. e. of the rd. to Soulsbyville, Epling 575 (5).

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